

Can. J. Genet. Cytol. 25: 430—436 (1983). — MITTON, J. B., LINHART, Y. B., STURGEON, K. B. and HAMRICK, J. L.: Allozyme polymorphisms detected in mature needle tissue of ponderosa pine. J. Hered. 70: 86—89 (1979). — O'MALLEY, D. M., ALLENDORF, F. W. and BLAKE, G. M.: Inheritance of isozyme variation and heterozygosity in *Pinus ponderosa*. Biochem. Genet. 17, 233—250 (1979). — ORNSTEIN, L.: Disk electrophoresis. I. Background and theory. Ann. N. Y. Acad. Sci. 121: 321—349 (1964). — RUDIN, D. and RASMUSON, B.: Genetic variation in esterases from needles of *Pinus sylvestris* L. Hereditas 73: 89—98 (1973). — RUDIN, D.: Inheritance of glutamate-oxalate-transaminases (GOT) from needles and endosperms of *Pinus sylvestris*. Hereditas 80: 296—300 (1975). — RUDIN, D.: Leucine-amino-peptidases (Lap) from needles and macro-gametophytes of *Pinus sylvestris* L. — Inheritance of allozymes —. Hereditas 85: 219—226 (1977). — RUDIN, D. and EKBERG, I.: Linkage studies in *Pinus sylvestris* L. — using macro gametophyte allozymes. Silvae Genet. 27: 1—12 (1978). — SCANDALIOS, J. G.: Genetic control of multiple molecular forms of enzymes in plants: A review. Biochem. Genet. 3: 37—79 (1969). — SHIRAIISHI, S. and KAMINAKA, H.: Substrate specificity of esterase and acid phosphatase isozymes in *Chamaecyparis obtusa* S. et Z. Bull. Kyushu Branch, Jap. For. Soc. 34: 97—98 (in Japanese) (1981). — WHEELER, N. C. and GURIES, R. P.: Population structure, genic diversity and morphological variation in *Pinus contorta* DOUGL. Can. J. For. Res. 12: 595—606 (1982). — YEH, F. C. and O'MALLEY, D.: Enzyme variations in natural populations of Douglas-fir, *Pseudotsuga Menziesii* (MIRB.) FRANCO, from British Columbia. I. Genetic variation patterns in coastal populations. Silvae Genet. 29: 83—92 (1980).

Monoterpene Analysis of a Diallel Cross in Sitka Spruce

By G. I. FORREST and C. J. A. SAMUEL

Forestry Commission, Northern Research Station,
Roslin, Lothian Region EH25 9SY, Scotland

(Received 21st July 1986)

Summary

The monoterpene composition of the cortical oleoresin of main stems and of branch apical shoots was analysed in the progeny of a complete diallel cross among seven trees of *Picea sitchensis*, and also in the parent trees and in half-sib open pollinated families. For the majority of the monoterpenes in each oleoresin system, practically all the significant variation was attributable to general combining ability, with the progenies reflecting the differences in parental means in additive combination with little significant deviation from this pattern due to specific combining ability or reciprocal effects. Non-additive variation was significant in three instances, in particular for α -pinene in main stem cortical oleoresin.

Key words: *Picea sitchensis*, Sitka spruce, oleoresin, monoterpenes, diallel cross, inheritance.

Zusammenfassung

Die Monoterpenzusammensetzung des Rindenzharzes des Stammes und der Hauptäste wurde bei *Picea sitchensis* Nachkommenschaften eines vollständigen Kreuzungsdiallel (7×7) sowie bei den Kreuzungspartnern und deren Nachkommenschaften — entstanden aus freier Abblüte — analysiert. Für die Mehrheit der Monoterpene in jedem Harzsystem ließ sich praktisch die gesamte Variation auf die generelle Kombinationseignung zurückführen, wobei die Nachkommenschaften die Unterschiede zwischen den Mittelwerten der Eltern bei additiver Kombination zeigten. Von diesem Muster gab es signifikante Abweichungen bedingt durch spezifische Kombinationseignung oder reziproke Effekte. Die nicht-additive Variation war in drei Fällen signifikant, besonders für α -Pinen im Rindenzharz des Stammes.

Introduction

The monoterpene compositions of the volatile needle oil and of the cortical oleoresin of Sitka spruce (*Picea sitchensis* (BONG.) CARR.) show a high degree of variation from tree to tree (VON RUDLOFF, 1977; FORREST, 1980a,b). Part of this variation has been shown to be due to the origin of the populations (FORREST, 1980b), but there remains a high within-population variation. In order that monoterpene characteristics can be used as genotypic indicators in studies of population variability, it is essential to investigate the ge-

notypic basis of this variation, and to determine the heritability of individual monoterpenes and their degree of freedom from environmental influence. The availability of the progeny of a complete diallel cross among seven trees of a Sitka spruce population provided the opportunity to carry out this form of analysis.

Heritability studies involving monoterpene data in conifers have been carried out on a number of species, but the majority have been concerned with pines rather than with spruces, and while there have been several reports on heritability estimates for individual monoterpenes, there appears to have been no biochemical work involving full diallel matings. Estimates of narrow-sense heritability, usually from regressions of progeny means on mid-parent values, and in some cases also of broad-sense heritability, have been made for the main monoterpenes in *Pinus monticola* DOUGL. (HANOVER, 1966, 1971), *P. elliotii* ENGELM. (SQUILLAGE, 1971), *P. taeda* L. (ROCKWOOD, 1973), *P. pinaster* AIT. (BARADAT *et al.*, 1975), *P. silvestris* L. (HILTUNEN, 1976), and *P. virginiana* MILL. (MEIER and GOGGANS, 1978). Generally heritability values were found to be high or very high, indicating a high degree of isolation from environmental effects. In the spruces, the only analysis known to the authors involving controlled crossings is that of ESTEBAN *et al.* (1976) for *Picea abies* (L.) KARST., from which it was postulated that the relative concentrations of α -pinene, α - + β -pinene, and 3-carene were each controlled by one gene locus having one dominant and one recessive allele. Indirect evidence from monoterpene percentage frequency histograms was obtained for the mode of genetic control of the levels of the cortical oleoresin monoterpenes in *Picea glauca* (MOENCH) Voss; smooth distributions for the pinenes and limonene suggested multiple gene control, while skewed distributions with indications of bimodality for 3-carene, myrcene and β -phellandrene suggested control by few genes (WILKINSON *et al.* 1971). Data on monoterpene inheritance in Sitka spruce are lacking.

Materials and Methods

The seven parents of the diallel cross were part of a small stand planted in Laigh of Moray Forest (Grampian Region, E Scotland) in 1933. The crossing programme was

carried out in 1968 as described by SAMUEL *et al.* (1972). Cortical oleoresin was sampled in October 1974 from replicate progeny plots planted at Bush Nursery 10 km south of Edinburgh (Lothian Region, National Grid Ref NT247640, elevation 185 m). Four trees were sampled from each of the 49 crosses, and also from seven half-sib families of each parent grown from open-pollinated seed collections in the same experiment. From each tree, cortical oleoresin was taken from the main stem at mid-height and from the apical shoot of a branch-whorl arising approximately mid-way up the mainstem. The compositions of the two oleoresin systems were treated as distinct characters in the analysis. The parent trees were sampled for cortical oleoresin from branch stems and from branch apical shoots in January 1980. Analysis of oleoresin samples was carried out by gas chromatography as previously described (FORREST, 1980a).

Results

Seven monoterpenes were recognised as constituents of the oleoresin samples, but two of these, camphene and 3-carene, were often undetectable. Indeed, among the 196 trees sampled in the full-sib families, camphene was absent from 67% and 3-carene from 74% of the main stem samples (each was present in 46% of the branch apical shoot samples), and for this reason further consideration of these two components will not be reported. Limonene was not detected in 17 main stem samples and 15 branch apical shoot samples; however, these deficiencies were not considered serious enough to prohibit analysis. The remaining four monoterpenes, α -pinene, β -pinene, β -phellandrene and terpinolene, were present in all samples in proportions ranging from around 2% in terpinolene to up to half the total monoterpene content in the case of β -phellandrene.

Frequency distributions for each of these five terpenes as percent of total monoterpenes were considered. α -pinene and β -pinene showed similar distributions although the distribution for α -pinene was positively skewed. The distribution for β -phellandrene was broad whilst that for terpinolene was narrow, neither of these showing any marked tendency to skewness. Limonene had a markedly positively skewed distribution with a tendency towards two modes, the more pronounced in the lower class.

Analysis of variance of diallel families

Family means for five monoterpenes are presented in Table 1a–j. The data given are the percentage contributions of each monoterpene to the total monoterpene content of the oleoresin. Table 1a–e concerns cortical oleoresin extracted from the main stem, while Table 1f–j contains data for cortical oleoresin from branch apical shoots. In each table, family means for the 49 families resulting from the 7 × 7 cross are displayed in a diallel pattern. A row mean is the mean across all the families in which a particular parent tree was used as a female parent; a column mean likewise for a parent tree used as a male parent. An overall mean is the mean of all families involving a parent tree as either male or female parent (or both). The leading diagonal contains data from the selfed families whilst the families either side of this diagonal are reciprocal crosses of one another. There were clear differences among the overall means for all monoterpenes and in general the ranking of the parents at this level was followed by their ranking in the row and column means. Selfed families were normally of the same order as crossed families and there were no obvious specific reciprocal differences.

The data for the five monoterpenes were analysed using the general analysis for diallel crosses suggested by GRIF-FING (1956) and the analyses of variance are summarised in Table 2a and b. The analysis is an extension of that for a randomised block in which the variation among families

Table 1. — Family means of individual monoterpene percentage values for cortical oleoresin.

1. MAIN STEM								
a. α -pinene								
Female parents	A	C	D	Male parents				Mean
				G	H	J	K	
A	24.1	16.9	17.0	19.6	15.0	15.6	17.4	17.9
C	17.5	13.7	16.6	16.7	17.3	17.0	13.8	16.1
D	18.4	16.1	25.0	19.8	18.8	18.5	15.6	18.9
G	19.4	15.5	20.3	23.7	23.9	17.9	19.2	20.0
H	27.2	18.3	20.4	22.9	17.9	15.9	16.7	19.9
J	18.6	13.1	17.1	17.2	19.9	15.2	15.2	16.6
K	14.9	15.6	15.6	17.1	21.0	16.6	16.2	16.7
Mean	20.0	15.6	18.9	19.5	19.1	16.7	16.3	18.0
Overall mean	19.0	15.8	18.9	19.8	19.5	16.6	16.5	
b. β -pinene								
Female parents	A	C	D	Male parents				Mean
				G	H	J	K	
A	20.6	24.5	23.3	22.0	26.0	26.5	22.9	23.7
C	22.9	28.3	24.1	23.6	26.3	27.8	26.7	25.7
D	23.7	23.7	20.9	20.3	20.3	23.2	26.2	22.6
G	20.4	23.8	19.9	18.9	20.0	23.6	23.2	21.4
H	20.8	22.0	21.8	18.9	23.0	29.4	21.8	22.5
J	24.5	31.6	24.1	23.1	24.6	26.9	27.2	26.0
K	22.4	22.6	25.9	22.2	25.0	24.1	22.3	23.5
Mean	22.2	25.2	22.9	21.3	23.6	25.9	24.3	23.6
Overall mean	22.9	25.4	22.7	21.3	23.1	26.0	23.9	
c. limonene								
Female parents	A	C	D	Male parents				Mean
				G	H	J	K	
A	1.23	0.55	0.83	0.98	4.33	0.48	4.03	1.77
C	1.00	0.38	0.95	0.50	0.70	0.65	7.03	1.60
D	1.58	1.70	1.48	1.58	7.35	1.73	4.28	2.81
G	1.06	0.58	1.65	0.88	11.00	0.65	9.98	3.69
H	6.10	5.48	6.40	7.83	3.18	4.68	13.20	6.69
J	0.88	0.65	0.90	0.68	8.73	0.50	9.20	3.08
K	10.63	9.78	4.78	6.03	7.78	13.78	12.25	9.29
Mean	3.21	2.73	2.43	2.64	6.15	3.21	8.56	4.13
Overall mean	2.49	2.16	2.62	3.16	6.42	3.14	8.93	
d. β -phellandrene								
Female parents	A	C	D	Male parents				Mean
				G	H	J	K	
A	51.6	54.0	55.5	54.3	49.5	52.0	52.1	52.7
C	55.0	51.2	53.6	55.3	49.9	48.4	46.6	51.4
D	52.5	54.0	46.9	55.8	51.2	51.1	47.8	51.3
G	56.4	54.0	53.9	54.5	42.4	53.3	42.6	51.0
H	42.7	50.4	47.2	48.2	51.9	42.2	43.6	46.6
J	51.7	46.6	53.3	54.9	41.4	51.4	41.6	48.7
K	47.4	45.8	47.3	50.3	40.0	40.2	43.7	44.9
Mean	51.0	50.9	51.1	53.3	46.6	48.4	45.4	49.5
Overall mean	51.9	51.3	51.2	52.2	46.6	48.5	45.2	
e. terpinolene								
Female parents	A	C	D	Male parents				Mean
				G	H	J	K	
A	2.08	3.80	3.35	2.70	5.18	5.53	3.45	3.73
C	3.13	6.20	4.18	3.58	5.35	6.00	5.78	4.89
D	3.75	4.13	3.05	1.93	2.28	4.10	5.85	3.58
G	1.90	4.00	2.18	1.15	2.60	4.00	4.35	2.88
H	2.75	3.63	3.53	1.80	3.93	7.65	4.23	3.93
J	4.28	8.00	4.28	3.58	5.35	5.90	6.85	5.46
K	4.13	4.35	5.80	3.58	5.50	5.30	4.68	4.76
Mean	3.14	4.87	3.76	2.61	4.31	5.50	5.03	4.18
Overall mean	3.43	4.87	3.67	2.74	4.11	5.48	4.89	

2. BRANCH APICAL SHOOTS

f. α -pinene

Female parents	A	C	D	Male parents				Mean
				G	H	J	K	
A	21.5	23.7	16.7	19.3	36.8	24.8	22.2	23.5
C	20.8	20.3	15.8	18.5	24.7	23.3	18.8	20.3
D	21.6	18.2	13.8	18.5	30.9	20.8	18.4	20.3
G	18.5	11.1	14.4	21.0	34.1	15.1	17.0	18.7
H	42.3	32.1	27.6	26.4	30.9	43.3	27.7	32.9
J	27.5	19.6	22.0	22.2	41.8	28.4	27.0	26.9
K	19.7	24.2	19.7	17.9	32.4	28.8	20.4	23.3
Mean	24.5	21.3	18.5	20.5	33.1	26.3	21.7	23.7
Overall mean	24.1	20.8	19.4	19.6	33.0	26.6	22.5	

g. β -pinene

Female parents	A	C	D	Male parents				Mean
				G	H	J	K	
A	17.6	18.7	18.4	19.1	17.8	19.1	18.0	18.4
C	19.6	20.8	17.7	18.8	17.8	18.9	18.6	18.9
D	18.3	19.0	15.6	18.1	17.5	17.1	18.8	17.8
G	18.7	16.4	16.8	18.6	16.7	18.6	15.9	17.4
H	16.8	17.7	15.9	16.7	16.9	18.5	15.2	16.8
J	19.4	24.0	18.3	19.0	17.2	19.6	17.6	19.3
K	16.2	17.1	16.1	18.4	15.8	15.8	15.9	16.5
Mean	18.1	19.1	17.0	18.4	17.1	18.2	17.1	17.8
Overall mean	18.2	19.0	17.4	17.9	16.9	18.7	16.8	

h. limonene

Female parents	A	C	D	Male parents				Mean
				G	H	J	K	
A	0.93	0.53	0.48	0.85	3.05	0.60	3.73	1.45
C	0.60	0.40	0.78	0.40	0.65	0.53	5.90	1.32
D	1.15	1.35	0.85	1.18	4.43	1.30	3.63	1.98
G	0.88	0.45	1.15	0.95	6.80	0.83	6.55	2.51
H	4.33	4.03	4.03	4.23	3.99	4.23	12.73	5.35
J	0.98	0.45	0.80	0.70	6.43	0.73	7.33	2.49
K	8.50	8.80	4.90	4.20	6.58	13.10	10.50	8.08
Mean	2.48	2.29	1.85	1.79	4.55	3.04	7.19	3.31
Overall mean	1.96	1.80	1.92	2.15	4.95	2.76	7.63	

i. β -phellandrene

Female parents	A	C	D	Male parents				Mean
				G	H	J	K	
A	46.4	47.7	47.0	48.0	39.6	46.7	49.9	46.5
C	54.5	56.9	45.0	52.1	47.7	46.0	50.5	50.4
D	48.5	53.0	35.3	47.0	41.0	38.9	48.1	44.5
G	48.0	40.0	44.4	47.1	34.0	44.3	36.5	42.0
H	33.1	45.0	36.8	40.4	42.5	32.0	36.9	38.1
J	46.2	53.3	45.1	46.7	32.7	47.9	42.2	44.8
K	43.4	43.8	38.6	48.7	33.7	33.9	39.6	40.2
Mean	45.7	48.5	41.7	47.1	38.7	41.4	43.4	43.8
Overall mean	46.1	49.4	43.1	44.6	38.4	43.1	41.8	

j. terpinolene

Female parents	A	C	D	Male parents				Mean
				G	H	J	K	
A	1.98	1.90	2.55	2.18	0.95	1.95	1.40	1.84
C	1.75	1.48	2.98	1.93	1.88	2.33	1.55	1.98
D	1.73	1.70	4.33	2.28	1.23	3.13	1.95	2.33
G	2.45	3.83	3.13	2.10	1.43	3.35	3.10	2.77
H	0.90	0.85	2.13	1.80	1.15	1.43	1.38	1.38
J	1.55	2.60	2.50	2.33	1.00	1.55	1.63	1.88
K	1.98	1.45	2.83	1.88	1.78	1.65	2.10	1.95
Mean	1.76	1.97	2.92	2.07	1.34	2.20	1.87	2.02
Overall mean	1.80	1.98	2.63	2.42	1.36	2.04	1.91	

has been partitioned into the first three items in the table. Mean squares together with the results of significance tests are given; the figure in parentheses below each mean square is the percentage contribution of the variance component for the same source to the overall phenotypic variance. Missing percentages indicate that the variance com-

ponent was negative upon estimation. It is clear that the general observations made on the data in Table 1a—j are supported by these analyses of variance. By far the greatest amount of significant variation was attributable to general combining ability (g.c.a.) which reflected the variation already observed among the overall means. G.c.a. was highly significant for all monoterpenes in both main stem and branch apical shoot extracts. Specific combining ability (s.c.a.) was significant for α -pinene in both main stem and branch apical shoot extracts and for β -phellandrene in main stem oleoresin only. It followed that when the means of reciprocal families were considered, there were significant departures among them from the expected values for monoterpane percentages obtained by summing the theoretical additive contributions of the parents. Clearly such effects are not easily seen from Table 1a—j, but the presence of significant s.c.a. does provide evidence of inheritance controlled by non-additive causes in addition to the strong additive control already identified and this effect was consistent at least for α -pinene. There were significant reciprocal effects for two monoterpenes, α -pinene from main stem oleoresin and β -pinene from branch apical shoots. The reciprocal effects can be partitioned into the contribution due to differences between row and column means among the parents and any further individual significant reciprocal deviations remaining. For main stem α -pinene, significant reciprocal differences were attributable to the latter cause whilst for branch apical shoot β -pinene they were due to the former. No obvious explanation of such differences was readily apparent and they must be considered as minor in relation to the overall patterns of inheritance which emerged from these analyses.

Parent/offspring relationships

The mode of genetic control of the inheritance of these terpenes could also be investigated from parent/offspring regressions since the results of the chemical analysis of resin samples from the individual parent trees were available together with analysis of the half-sib open-pollinated families grown in the same experiment as the full-sib diallel families. The data resulting from these analyses are presented in Table 3 from which it can be seen that, although for a number of terpenes a smaller overall proportion was found in parents than in half-sib families, similar relative levels among the seven parent trees were found in each. The single notable exception to this was α -pinene in main stems where this pattern was clearly broken. The regressions of offspring on parent were calculated for each terpene and adjustments made by the methods of FRANKLIN (1974) to obtain heritability values. A similar approach was to consider the regressions of full-sib family means on calculated mid-parent values. These data are not presented.

Heritability estimates from both these approaches are presented in Table 4 together with a further estimate derived from the variance components estimated in the extension of the analysis of variance. These components were given as proportions of phenotypic variance in Table 2 and since the variance component for g.c.a. estimates one quarter of the additive variance, the estimates of narrow-sense heritability in Table 4 are four times the proportions in Table 2. Most of the estimates in Table 4 continued to support the previous evidence of a strong additive mode of inheritance for all monoterpenes considered. The most notable exception to this general pattern was α -pinene from main-stem resin, for which, in the earlier analysis of variance, there

Table 2. — Analysis of variance of the data summarised in Table 1a—j.

a. Main stem oleoresin	df	Mean squares (variance components %)				
		A	B	C	D	E
General combining ability	6	148.00*** (13.8)	146.17*** (17.4)	363.97*** (19.7)	431.68*** (18.2)	51.794*** (23.4)
Specific combining ability	21	20.00* (7.1)	13.30 (2.9)	26.73 (1.2)	59.40** (13.4)	3.376 (2.6)
Reciprocal effects	21	22.41* (8.0)	12.94 (2.2)	16.46 —	21.45 —	2.928 (1.0)
Blocks	3	35.21	8.66	25.23	21.49	0.515
Error	144	11.77 (71.1)	10.56 (77.5)	24.21 (79.1)	24.97 (68.4)	2.702 (73.0)
b. Branch apical shoot oleoresin	df	Mean squares (variance components %)				
		A	B	C	D	E
General combining ability	6	1302.43*** (34.4)	41.12*** (14.8)	271.45*** (22.8)	669.43*** (15.2)	9.548*** (12.2)
Specific combining ability	21	85.29** (8.8)	4.02 (2.1)	11.58 —	77.63 (5.4)	1.061 —
Reciprocal effects	21	38.39 —	6.27* (8.1)	12.89 —	83.13 (5.7)	1.273 (2.2)
Blocks	3	45.21	9.48	19.79	32.50	0.320
Error	144	40.88 (56.8)	3.36 (75.0)	15.68 (77.2)	51.39 (73.7)	1.060 (85.6)

Key to monoterpenes: A, α -pinene; B, β -pinene; C, limonene; D, β -phellandrene; E, terpinolene.
* $p = 0.05-0.01$; ** $p = 0.01-0.001$; *** $p < 0.001$.

Table 3. — Mean percentages of total monoterpenes for the 5 components in parent trees and in half-sib families.

Main stem	Monoterpene											
	A		B		C		D		E			
	P	F ₁	P	F ₁	P	F ₁	P	F ₁	P	F ₁		
A	12.2	15.9	20.1	20.1	0.16	9.23	50.5	51.7	3.17	3.05	A	
C	13.3	16.7	21.8	25.6	0.00	1.38	61.5	51.6	2.60	4.35	C	
D	12.5	21.4	21.0	22.7	0.16	2.93	54.1	48.3	3.39	3.40	D	
G	13.5	19.2	19.9	20.2	0.11	2.89	57.8	53.2	1.86	2.25	G	
H	25.0	18.2	20.2	22.2	6.12	12.93	46.8	40.4	1.05	4.05	H	
J	16.6	15.3	23.8	25.2	0.05	3.80	54.6	49.9	4.08	5.23	J	
K	12.3	14.0	21.1	20.7	7.20	20.58	45.2	40.5	4.96	4.28	K	
Apical shoots	P		F ₁		P		F ₁		P		F ₁	
A	9.7	20.6	21.9	16.0	0.39	9.58	37.7	43.8	4.02	1.65	A	
C	14.7	24.5	21.0	20.4	0.00	1.28	62.8	52.2	1.14	1.23	C	
D	8.5	17.5	18.2	16.4	0.00	1.70	40.1	38.9	3.56	3.50	D	
G	9.9	16.1	26.0	17.1	0.18	1.40	38.0	47.4	3.24	2.50	G	
H	32.0	35.2	19.0	16.2	5.34	9.90	42.8	35.3	0.37	0.85	H	
J	21.3	22.8	24.4	17.7	0.08	2.73	52.1	42.0	1.63	2.25	J	
K	9.7	21.7	18.1	14.8	3.31	19.30	35.9	40.0	4.15	1.10	K	

Key to monoterpenes: see footnote to Table 2. P, parent tree; F₁, half-sib family.

Table 4. — Heritability estimates by three different methods compared.

	α -pinene	β -pinene	limonene	β -phellandrene	terpinolene	
Main stem oleoresin	Parent-half sib	0.09	1.00	1.00	1.00	0.49
	Mid parent-full sib	0.16	0.71	0.85	0.58	0.40
	Variance components	0.83	0.94	0.94	0.56	0.96
Branch apical shoot oleoresin	Parent-half sib	0.89	0.42	0.98	0.72	0.49
	Mid parent-full sib	0.85	0.40	0.71	0.35	0.30
	Variance components	0.78	0.83	0.95	0.93	0.91

were significant reciprocal effects. If the full-sib/mid-parent regression was recalculated using the smaller set of reciprocal family means on their associated mid-parent values, the heritability estimate rose to 0.85; nevertheless, the low estimate from the half-sib/parent regression remained.

Discussion

The material available for the direct study of mode of inheritance of important traits in Sitka spruce in Britain is

limited, particularly when consideration of non-additive effects is an objective. The experimental material considered here, among the first full-sib families to be studied in this species, does have limitations previously intimated by SAMUEL *et al.* (1972) in that the parents were selected in a small stand of unknown seed origin and silvicultural history. Nevertheless, they were selected chiefly on the basis of fecundity and compatibility in crossing; thus in relation to vigour and more particularly to those chemical

traits considered here, the parent trees must be close to a random sample.

The main statistical consideration of the data resulting from these chemical analyses has been through standard analysis of variance for a set of diallel families. From this, and from further analysis based on parent/offspring regressions, the strongest feature to emerge has been the preponderance of highly significant additive control of all the traits measured. Evidence of non-additive variation was significant in three instances and was consistently so for α -pinene. In main stem oleoresin the proportion of additive variance for α -pinene was the lowest in a range of 13.8—23.4% whilst in branch apical shoot oleoresin it was highest in a range of 12.2—34.4%. This means that the presence of non-additive variation in some instances was not generally associated with a diminution of additive variation. Where significant non-additive variation was present, the ratio of additive to non-additive variance components varied from 1.4 to 3.9 whereas for the remainder of the terpenes considered it lay between 6.1 and 16.8.

It should be pointed out that, in the light of a critique by BIRKS and KANOWSKI (1988) of the methods of treatment of percentage data which are generally used in coniferous resin analysis, the numerical aspects of the present analysis should be viewed with caution. Nevertheless, we feel that our general conclusions are valid, particularly as a mere visual inspection of the raw percentage data suffices to demonstrate the close relationship between parental and progeny resin composition. Moreover, it is not apparent that any more rigorous means of treatment of such data is at present available.

This general evidence on the mechanism of control of inheritance of the monoterpene constituents of oleoresin in this species can provide the basis of any programme of selection in relation to these traits. Should it become necessary, through for example the establishment of any relationships between terpenes and traits of economic importance, to select for an increase or decrease in any one of the terpenes considered here, the fairly high levels of ad-

ditive variation found would ensure a good response to selection under any selection scheme designed to exploit such variation. In addition, there could be further gains from the incorporation of schemes to exploit the non-additive variation in those instances where it is present.

Literature Cited

- BARADAT, P., BERNARD-DAGAN, C., PAULY, G. and ZIMMERMANN-FILON, C.: Les terpènes du pin maritime; aspects biologiques et génétiques. III. Hérité de la teneur en myrcène. *Ann. Sci. forest.* **32**: 29—54 (1975). — BIRKS, J. and KANOWSKI, P.: Interpretation of the composition of coniferous resin. *Silvae Genet.* **37**: 29—39 (1988). — ESTABAN, I., BERGMANN, F., GREGORIUS, H.-R. and HUHTINEN, O.: Composition and genetics of monoterpenes from cortical oleoresin of Norway spruce and their significance for clone identification. *Silvae Genet.* **25**: 59—66 (1976). — FORREST, G. I.: Seasonal and spatial variation in cortical monoterpene composition of Sitka spruce oleoresin. *Can. J. For. Res.* **10**: 452—457 (1980a). — FORREST, G. I.: Geographic variation in the monoterpene composition of Sitka spruce cortical oleoresin. *Can. J. For. Res.* **10**: 458—463 (1980b). — FRANKLIN, E. C.: Adjustment of heritabilities estimated by correlation coefficients for typical forest tree breeding experiments. *Silvae Genet.* **23**: 176—180 (1974). — GRIFPING, B.: Concept of general and specific combining ability in relation to diallel crossing systems. *Austr. J. Biol. Sci.* **9**: 463—493 (1956). — HANOVER, J. W.: Genetics of terpenes. I. Gene control of monoterpene levels in *Pinus monticola* DOUGL. *Heredity* **21**: 73—84 (1966). — HANOVER, J. W.: Genetics of terpenes. II. Genetic variances and interrelationships of monoterpene concentrations in *Pinus monticola*. *Heredity* **27**: 237—245 (1971). — HILTUNEN, R.: On variation, inheritance and chemical interrelationships of monoterpenes in Scots pine (*Pinus silvestris* L.). *Ann. Acad. Scient. Fenn., Series A IV*, **208**: 1—54 (1976). — MEIER, R. J. and GOGGANS, J. F.: Heritabilities and correlations of the cortical monoterpenes of Virginia pine (*Pinus virginiana* MILL.). *Silvae Genet.* **27**: 79—84 (1978). — ROCKWOOD, D. L.: Variation in the monoterpene composition of two oleoresin systems of loblolly pine. *For. Sci.* **19**: 147—153 (1973). — VON RUDLOFF, E.: Variation in leaf oil terpene composition of Sitka spruce. *Phytochem.* **17**: 127—130 (1977). — SAMUEL, C. J. A., JOHNSTONE, R. C. B. and FLETCHER, A. M.: A diallel cross in Sitka spruce. Assessment of first year characters in an early glasshouse test. *Theor. appl. Genet.* **42**: 53—61 (1972). — SQUILLACE, A. E.: Inheritance of monoterpene composition in cortical oleoresin of slash pine. *For. Sci.* **17**: 381—387 (1971). — WILKINSON, R. C., HANOVER, J. W., WRIGHT, J. W. and FLAKE, R. H.: Genetic variation in the monoterpene composition of white spruce. *For. Sci.* **17**: 83—90 (1971).

Juvenile Performance in a Range-Wide Provenance Test of *Fraxinus pennsylvanica* Marsh.¹⁾

By K. C. STEINER, M. W. WILLIAMS, D. H. DEHAYES,
R. B. HALL, R. T. ECKERT, W. T. BAGLEY, W. A. LEMMIEN,
D. F. KARNOSKY, K. K. CARTER and F. C. CECH²⁾

(Received 3rd November 1986)

1) Journal Paper No. 7441 of the Pennsylvania Agricultural Experiment Station. This research was supported in part by the U.S. Department of Agriculture, Cooperative Regional Project NE-27, and in part by Grant No. 23-773 from the U.S. Forest Service, Consortium for Environmental Forestry Studies.

2) Respectively, School of Forest Resources, Pennsylvania State University; Northeastern Forest Experiment Station, U.S. Forest Service; Department of Forestry, University of Vermont; Department of Forestry, Iowa State University; Department of Forest Resources, University of New Hampshire; Department of Forestry, University of Nebraska; Department of Forestry, Michigan State University; Department of Forestry, Michigan Technological University; College of Forest Resources, University of Maine; and Division of Forestry, West Virginia University. Direct correspondence to: KIM C. STEINER, 313 Forest Resources Laboratory, University Park, Pennsylvania 16802, U.S.A.

Summary

Height growth, winter injury, and incidence of flowering through age six from seed are described for 60 provenances of *Fraxinus pennsylvanica* planted at ten locations in Iowa, Maine, Michigan, Nebraska, New Hampshire, New York, Pennsylvania, Vermont, and West Virginia.

With few exceptions, the tallest trees at age six originated in two areas: southern Ontario and a "central prairie" region extending from eastern Nebraska to central Illinois. There was no consistent growth advantage in trees originating south of planting sites, and near-local provenances were in general only marginally taller than plantation means.